

Wear biomechanics in the slicing dentition of the giant horned dinosaur *Triceratops*

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Herbivorous reptiles rarely evolve occluding dentitions that allow for the mastication (chewing) of plant matter. Conversely, most herbivorous mammals have occluding teeth with complex tissue architectures that self-wear to complex morphologies for orally processing plants. Dinosaurs stand out among reptiles in that several lineages acquired the capacity to masticate. In particular, the horned ceratopsian dinosaurs, among the most successful Late Cretaceous dinosaurian lineages, evolved slicing dentitions for the exploitation of tough, bulky plant matter. We show how *Triceratops*, a 9-m-long ceratopsian, and its relatives evolved teeth that wore during feeding to create fullers (recessed central regions on cutting blades) on the chewing surfaces. This unique morphology served to reduce friction during feeding. It was achieved through the evolution of a complex suite of osseous dental tissues rivaling the complexity of mammalian dentitions. Tribological (wear) properties of the tissues are preserved in ~66-million-year-old teeth, allowing the creation of a sophisticated three-dimensional biomechanical wear model that reveals how the complexes synergistically wore to create these implements. These findings, along with similar discoveries in hadrosaurids (duck-billed dinosaurs), suggest that tissue-mediated changes in dental morphology may have played a major role in the remarkable ecological diversification of these clades and perhaps other dinosaurian clades capable of mastication.

INTRODUCTION

Large herbivorous vertebrates allow the examination of myriad topics from coevolution and escalation with evolving plant communities to the origin of novelty and morphological constraint (1). Previously, most of these studies have concentrated on mammals because of their extraordinarily complex dentitions with extensive occlusal topography and diverse tissue types. During their 300+-million-year diversification, reptiles (Sauria) rarely approached the biomechanical feeding sophistication seen in mammals (2–5). Reptilian teeth are typically simple semiconical, flattened recurved, or leaf-shaped structures. In most cases, the constrained jaw (adductor) musculature and quadrate-articular joint permit little more than orthal scissoring during jaw closure, and the teeth do not occlude (6–16). Consequently, the teeth are primarily used for seizing and for the coarse slicing or crushing of plants or prey (10, 12, 15, 16). Most reptile tooth crown architectures are simple, with only hard enamel surrounding a softer orthodontine core (7, 11, 14).

Nearly all mammals have multi-cusped teeth that are drawn across one another during chewing cycles (mastication) (8, 10, 15, 17, 18). This allows oral processing of plant and animal parts, facilitating rapid digestion (10, 15, 17). Their teeth self-wear [because of pressures generated from tooth-tooth contacts, entrapped food, and exogenous/endogenous abrasives (4, 18–22)], producing topographies, and generating differential pressures that split, crush, and drive fissures through food (4, 8, 10, 14, 18–22). This allows for dietary variability and specialization (10, 18). This capacity is rare in reptiles (4, 6) and was facilitated by the evolution of specialized dental tissues with unique synergistic wear and fracture attributes.

Dinosaurian radiation was exceptional among reptiles in that four convergent instances of precise dental occlusion evolved—in heterodontosaurid ornithomorphs, hadrosaurid duck-billed dinosaurs, giant sauropods, and ceratopsian horned dinosaurs (23–44). The latter three became dominant herbivorous terrestrial groups during the late Mesozoic Era, whose advanced dentitions allowed them to exploit a diversity of flora, including perhaps angiosperms that were diversifying at the same time (45). Primitive ceratopsians have low-angled shearing cheek teeth. Advanced ceratopsians (the clade encompassing Protoceratopsidae + Ceratopsidae) evolved distinctive high-angled slicing dentitions, allowing oral processing of tough and bulky plant matter.

Previous evidence points to a complex architecture promoting mammal-like self-wear in this group. In descriptions of ceratopsid dentitions from the early 1900s, “cementum” and “cementum-like” were used interchangeably to describe tissue adhering to the roots and possibly exposed on the slicing planes (46). Coronal cementum is a highly derived crest-supporting and basin-forming tissue in mammals (4). If present in ceratopsians, it represents only the second case of the independent evolution of this tissue in reptiles. In addition, they described the central portions of worn teeth becoming “bowled-out,” suggesting self-wearing functionality. We posit that the resultant fuller-like structures [a recessed central region like that seen in some swords and knives (47)] would have served to improve chewing efficiency. Not only do the structures reduce the contact area between the teeth and fodder (plant matter being chewed), but recessions also reduce the energy required to separate the tooth and plant fodder surfaces.

We use morphological, histological, and biomechanical data analyzed in a phylogenetic context to show that *Triceratops horridus* [Ceratopsidae: Chasmosaurinae—a large (up to 9-m total length) horned herbivorous dinosaur from the Latest Cretaceous of North America] (Fig. 1A) with fullers on the slicing dentition (Fig. 1, B and C) (46, 48)] (i) have crowns composed of a remarkable diversity of tissues, (ii) preserve wear properties, and (iii) formed surfaces with fullers due to inter-tissue differences in those properties (revealed using a wear simulation).

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Our findings suggest that changes in dental morphology and diet in ceratopsian dentitions were mediated through the evolution of new dental tissues. This facilitated their co-domination with hadrosaurids (which also show sophisticated dental architecture and biomechanics) of Late Cretaceous terrestrial herbivorous niches in Europe, Asia, and North America (46, 48–51).

RESULTS

Our results show that the occlusal surfaces of *Triceratops* teeth are much more complex than previously realized (Fig. 2A). The primitive reptilian tissues, enamel and orthodentine, as well as derived coronal cementum are present (44, 46). Enamel forms the prominent slicing edges (Fig. 2B). Orthodentine forms the planar slicing faces that extend around the mesial and distal edges of the occlusal surfaces (Fig. 2D). The cementum-like tissue reported by Hatcher and colleagues (46) is confirmed to be cellular cementum as evidenced by dark voids representing cementocyte lacunae (Fig. 2C). Its presence on the occlusal planes as a load-bearing surface [making it coronal cementum (8)] was also confirmed. This tissue's footprint extends from the mesial and distal ends of each enamel shell around the occlusal faces. Two formerly unidentified wear-relevant constituents are also present. The most prominent is independently derived vasodentine (dentine with branching vascularization), an unusual tissue not seen previously outside of osteichthyan fishes (14) (Fig. 2E). This material corresponds with the fuller-like basins that form in the middle of the occlusal faces of the teeth. Finally, there is a wear-resistant layer of hard mantle dentine, a tissue we also identified in hadrosaurid dinosaur teeth (4) (Fig. 2, A and C). It is composed of orthodentine lacking incremental lines of von Ebner, which make it appear amorphous when viewed with dissecting microscopy. It is found adjacent to the enamel shells and surrounds the orthodentine cores. Topographically, it corre-

sponds with the slicing faces established by the enamel and shallow rims around non-enamelled portions of each tooth's slicing face.

Tribology experimentation reveals the specific wear rates of the *Triceratops* dental tissues (Fig. 3). Wear rates range from $\sim 4.0 \times 10^{-5} \text{ mm}^3/(\text{N mm})$ for coronal cementum (highest wear rate, least wear-resistant) to $\sim 6.8 \times 10^{-6} \text{ mm}^3/(\text{N mm})$ for enamel (lowest wear rate, most wear-resistant). These values are comparable to wear rates previously reported on hadrosaurids and extant ungulate mammals (4). Like these taxa, the wear rates correspond to topographic features on worn batteries. Notably, the *Triceratops* vasodentine correlates with the deep centrally located basins previously observed in ceratopsian teeth (46).

The vasodentine has a wear rate about 1.6 times higher than orthodentine [$K \sim 3.1 \times 10^{-5} \text{ mm}^3/(\text{N mm})$ and $1.9 \times 10^{-5} \text{ mm}^3/(\text{N mm})$, respectively]. However, the hardness (determined via nanoindentation) for *Triceratops* vasodentine and orthodentine is statistically indistinguishable at a 0.5 level of significance ($n \geq 25$ indents per tissue). The *Triceratops* tissues reveal mean hardness values of 3.1 GPa for vasodentine, 3.5 GPa for orthodentine, 5.3 GPa for mantle dentine, 5.6 GPa for enamel, and 1.7 GPa for coronal cementum (Fig. 3C). These values are similar in magnitude, and, with regard to abrasive wear, they are in the exact relative hardness order (from hardest to softest) to those found for comparable tissues in extant horses and bison [coronal cementum, 0.4 to 1.0 GPa; orthodentine, 0.6 to 2.2 GPa; and enamel, 3.0 to 5.4 GPa (4, 52)]. This supports our contention, as we found in hadrosaurids (4), that tribological signatures in these fossil teeth are preserved.

Input of the measured wear rate values into the tribological model incorporating all of the five tissues (Fig. 4A) results in a three-dimensional topography seen in naturally worn *Triceratops* dental batteries (Fig. 4B). This includes enamel, mantle dentine, and orthodentine, which form high-relief cutting edges on the leading face and sides of worn teeth, and vasodentine, which forms a low relief basin.

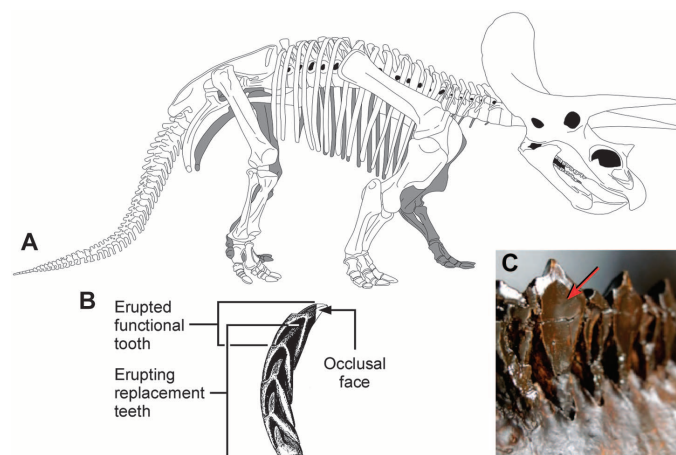


Fig. 1. *T. horridus* skeleton and dentitions. (A) *Triceratops* skeleton. (B) Transverse view of a dentary (lower jaw) tooth family in this dinosaur whose functional teeth wore to vertical slicing faces. The stippling depicted on the bifid roots is the cementum-like tissue described by Hatcher and colleagues (46). Image from (46) used with permission. (C) Naturally worn slicing teeth in the lower jaw of MOR 129734 showing the wear-induced bowing out of the central regions of the occlusal faces of the teeth (arrow) to form fuller-like implements.

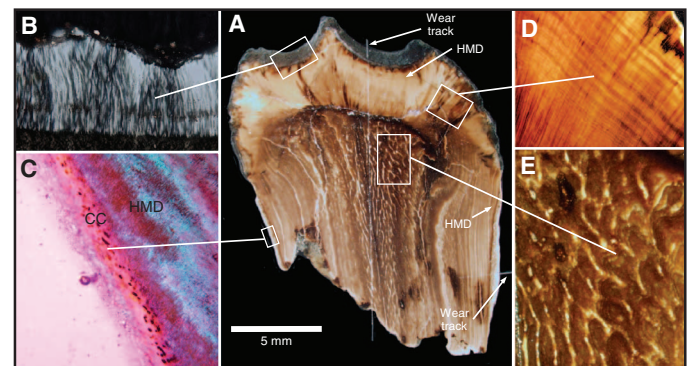


Fig. 2. *Triceratops* tooth crown histology. (A) Occlusal plane section of AMNH FARB 32189 viewed with dissecting microscopy showing the entire complement of osseous tissue constituents. Wear tracks from the reciprocating tribological testing are shown. HMD, hard mantle dentine. (B) Enamel shell viewed with polarized microscopy with a λ wave plate filter. (C) Coronal cementum (CC) adjacent to the hard mantle dentine viewed with polarized microscopy with a λ wave plate. The dark granules represent cementocyte lacunae. The outermost layer lacks such structures and is composed of acellular cementum. (D) Orthodentine viewed with polarized microscopy with a λ wave plate showing dozens of daily formed incremental lines of von Ebner (28) (dark and light repeated bands spanning from upper left to lower right). (E) Vasodentine viewed with dissecting microscopy showing reticulated vascular canals (white structures) that once housed blood vessels.

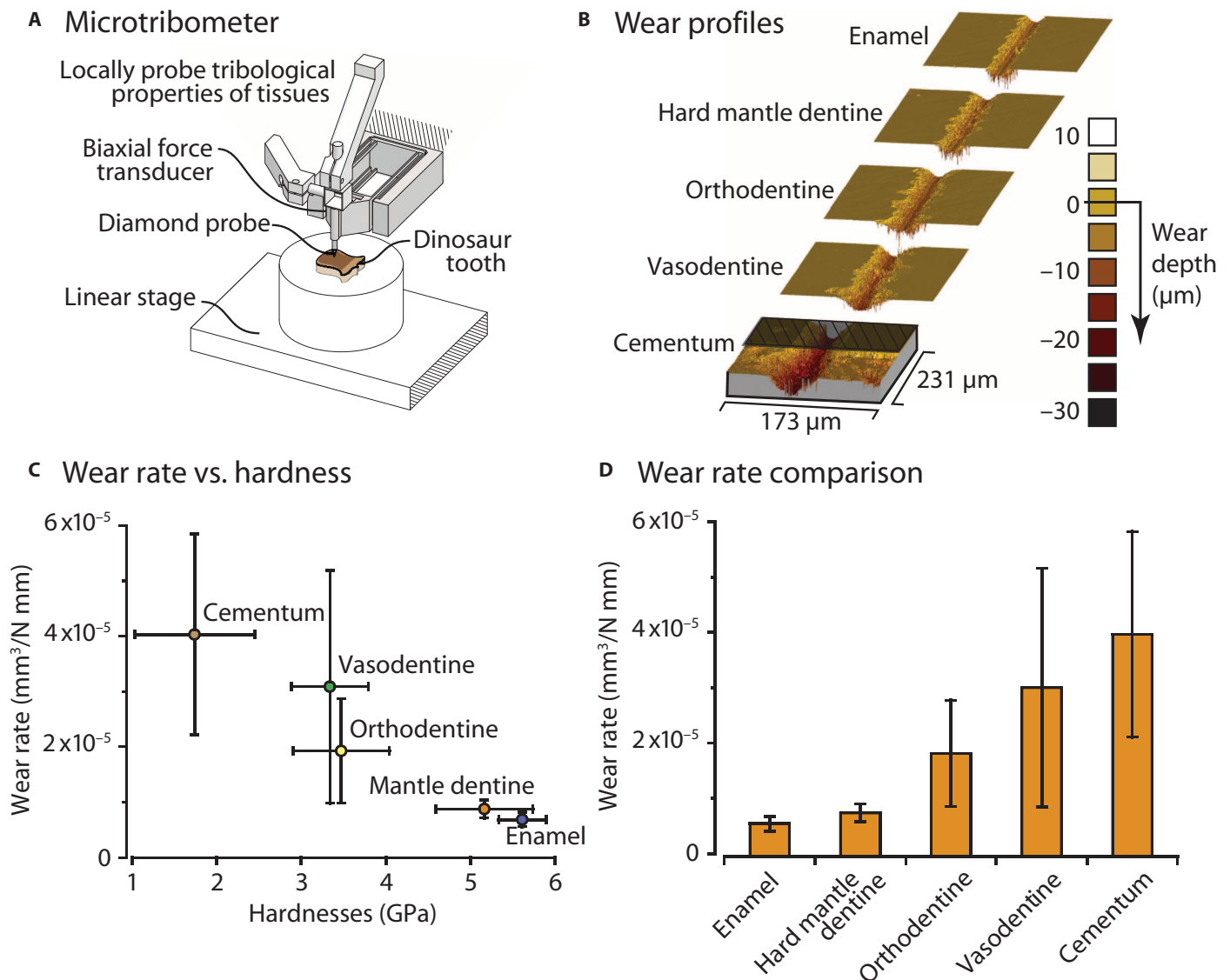


Fig. 3. Microtribology wear measurements. (A) Microtribometer used to slide a diamond-tipped probe across polished cross-sections of the fossilized teeth and to evaluate tissue wear rates. (B) Topographic profiles of wear scars created in various tissues by the sliding diamond probe. (C) Hardness of tissues versus wear rate for each ceratopsian dental tissue ($n \geq 25$ per tissue). (D) Average *Triceratops* dental tissue wear rates. Error bars $\pm 1 \sigma$.

Collectively, this produced a tooth form with fullers. Models reveal the contributions of each tissue to the worn topography and show that the overall morphology is impossible to achieve without the ensemble contributions of enamel, mantle dentine, orthodentine, and vasodentine (Fig. 4, D to G).

Coronal cementum, unlike in ungulate mammals and hadrosaurids (4, 8, 18, 20), has a very small footprint on the chewing surface. In those herbivores it is bounded by other tissues across the occlusal face and can contribute to basin formation. (4) (Fig. 4C). The root cementum in *Triceratops* acted to bind the roots of the teeth together in the battery during eruption and the coronal cementum extended the length of the slicing stroke [roles also seen in hadrosaurids (4)]. The latter also likely supported the hard, brittle mantle dentine rim in a similar manner to its functionality in herbivorous mammals supporting enamel crests (4).

Vasodentine was the primary contributor to the formation of fuller relief basins on each tooth (Fig. 4). The use of a two-tissue orthodentine and enamel input [the primitive reptilian condition thought to characterize most dinosaur teeth (4, 14)] yields model results lacking a fuller (Fig. 4D). The basin also does not form when vasodentine is replaced with orthodentine (Fig. 4E). Input models with vasodentine, but without mantle dentine (Fig. 4F) or enamel (Fig. 4G), still form a fuller. This shows that vasodentine is primarily responsible for fuller formation in *Triceratops* teeth.

Character mapping of dental tissues and consideration of the bio-mechanical role of each tissue based on the *Triceratops* wear model show that the primitive amniote tissues of an enamel shell surrounding an orthodentine core with root cementum were retained through the clade's evolution of variably angled, slicing-shearing dental occlusion

seen in Psittacosauridae. The cladogenesis of Leptoceratopsidae + Protoceratopsidae + Ceratopsidae signaled the advent of same-angled shearing cheek teeth (low-angled in Leptoceratopsidae, high-angled in Protoceratopsidae + Ceratopsidae) and enamel loss opposite the leading slicing edges of the teeth. This arrangement promoted the formation of sharp cutting edges because of enamel being the most wear-resistant tissue. Hard mantle dentine, with remarkably low wear rates for a dentine, extended the cutting planes around the occlusal faces of the teeth. Root cementum moved onto the chewing faces, becoming coronal cementum, likely serving to support brittle mantle dentine rims. In Protoceratopsidae + Ceratopsidae, vasodentine appeared in the cores of the teeth and promoted the formation of the fuller-like

basins, reducing friction and diminishing the requisite jaw adductor force to slice plant matter. The coronal cementum became much thicker, presumably to solidify the erupting dental batteries so they could act as unified slicing implements and have increased chewing stroke length (Fig. 5).

DISCUSSION

The results show that ceratopsian tooth crowns were histologically more complex than appreciated. They were composed of five major wear-relevant osseous tissues (enamel, hard mantle dentine, orthodentine, vasodentine, and coronal cementum). This tissue diversity exceeds the most complex mammalian dentitions such as those of ungulates, which are composed of four wear-relevant constituents (enamel, orthodentine, secondary dentine, and coronal cementum) (4, 19, 20). This is the second dinosaurian clade [the other being Hadrosauridae (4, 29)] where complexity beyond typical reptiles is demonstrated. The complexity of ungulate mammalian teeth involving tissue attributes with structural and wear attributes allowing for self-wear to complex morphologies may have promoted dietary diversification during their evolutionary radiations (20). Correlations of ceratopsian tissue ensembles with topographical features on the occlusal faces of the teeth (for example, basins, rims, and slicing faces) tooth form character mapping suggest that, as in mammals and hadrosaurids (4), evolution of novel tissues with specific biomechanical attributes may have played a major role in dietary diversification. We anticipate that other dinosaurs (for example, Sauropoda and Heterodontosauridae) and perhaps other reptiles that evolved precise dental occlusion [Rhynchocephalia (2, 3)] will be found to have complex dental architecture. Clade-specific complexity

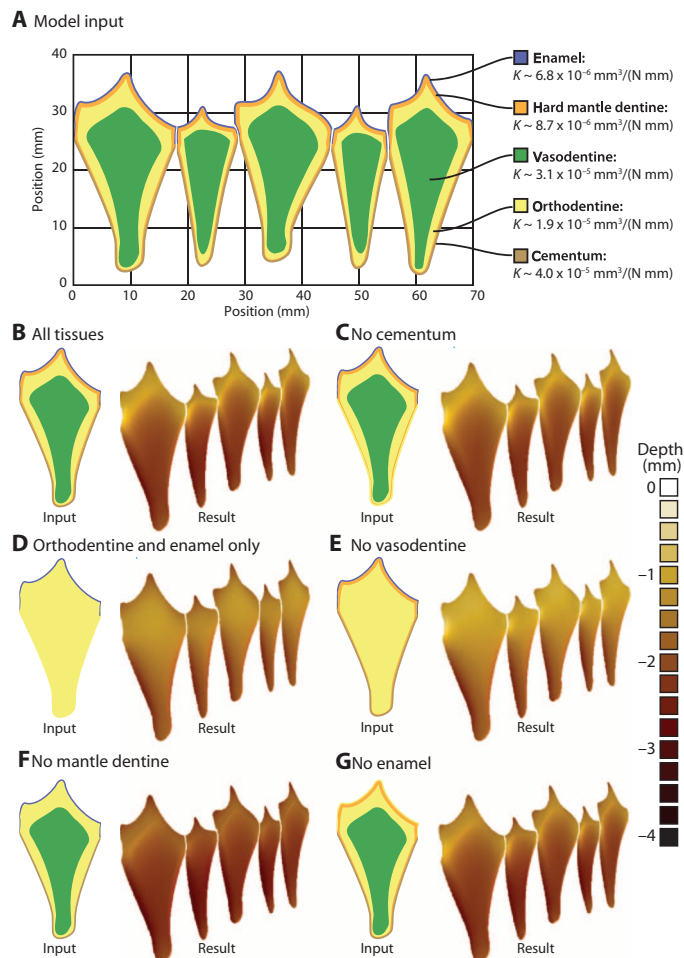


Fig. 4. Tooth wear simulation. (A) Initial dental tissue distribution used in the Matlab wear model. (B to G) Model result considering (B) all tissues [note: the rendering mimics the naturally worn occlusal faces of *Triceratops* teeth including recovery of a basin caused by the relatively fast-wearing vasodentine (see Fig. 1C)], (C) a dentition without cementum showing negligible topographical difference from the all tissue rendering, (D) a tooth composed of just primitive amniote orthodentine and enamel typical of reptiles showing a lack of a fuller basin, (E) a dentition without vasodentine showing an absence of recession in the middle of the tooth, (F) a dentition without mantle dentine showing a slightly shallower plateau developed near the tip of the tooth, and (G) a dentition without enamel resulting in a blunter cutting edge and overall more rounded occlusal face.

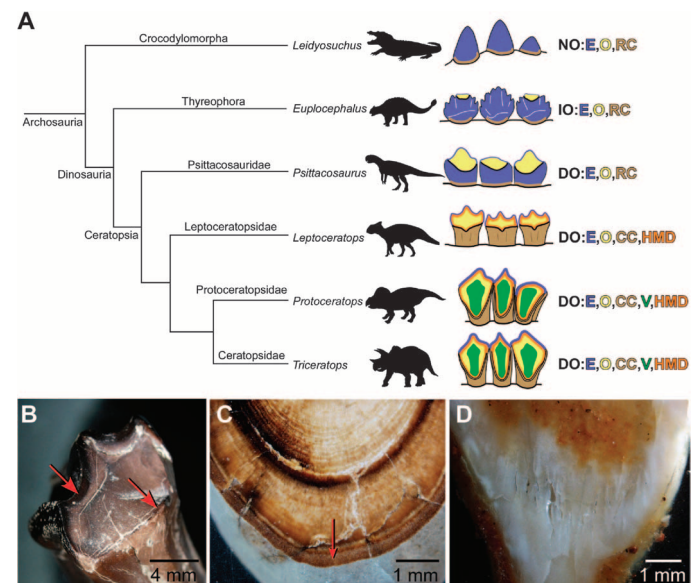


Fig. 5. Dental tissue evolution in Ceratopsia. (A) Phylogenetic hypothesis for Ceratopsia (50, 56, 57) with character mapping of degrees of dental occlusion and osseous tissues. NO, non-occluding dentition; IO, incipient occlusion; DO, dental occlusion; E, enamel; O, orthodentine; RC, root cementum; CC, coronal cementum; HMD, hard mantle dentine; V, vasodentine. (B) Mantle dentine in *Leptoceratops* (dark tissues denoted by arrows; UAMES 34151). (C) Coronal cementum in *Leptoceratops* (AMNH FARB 32188). (D) Vasodentine (tissue with voids) in *Protoceratops* (AMNH FARB 6251).

of reptilian teeth can provide a rich new source of characters for use in phylogenetic studies.

A notable finding from our study is that the tissue suites acquired by Ceratopsia are novel with regard to type and function. Most notable is that the cores of advanced ceratopsian teeth are constructed of vasodentine. Vasodentine's exceptional porosity promoted unusually high wear rates to form fullers (Fig. 4B). The porosity of this tissue reduces the overall structural integrity by causing stress concentrations, leading to the localized fracture and massive removal of material (53, 54). This is a unique strategy among tetrapods for creating advanced tooth topography.

Ceratopsian evolution of coronal cementum is also novel. This represents only the second instance where this tissue, commonly found in ungulates, has been found in reptiles, the other being its independent derivation in hadrosaurid dinosaurs (4, 29). Notably, coronal cementum has been used as evidence of mammalian teeth being architecturally and biomechanically more sophisticated than those of reptiles (14).

Our discovery of preserved tribological attributes in Ceratopsia represents the second time such properties have been recovered from fossil dinosaur teeth. This, along with similar recovery from Pleistocene mammalian fossils (4) and our ability to model wear in both extant and fossil grinding dentitions, and now slicing teeth, point to a rich new avenue for exploration of dental biomechanics in a diversity of vertebrates. We stand to gain a more comprehensive understanding of how animals adapted to exploit new diets throughout time (2, 3, 5). Also, it is notable that our paleontologically driven tribological questions, such as those explored here, resulted in development of new engineering tools and computational models that can be applied to academic and commercial engineering applications (4, 55).

METHODS

Overview

We conducted a series of morphofunctional analyses on the *Triceratops* dentition by (i) characterizing the morphology of in situ teeth within dental batteries [interlocking developing and functional teeth that erupt to form unified chewing surfaces (7)], (ii) histologically characterizing the tissue types and their three-dimensional distributions throughout the teeth, (iii) conducting wear and nanohardness testing to reveal tribological tissue attributes, (iv) making wear models of the occlusal surfaces to infer how self-wear to slicing implements occurred, and, finally, (v) studying the dental histology and morphology in outgroups to reconstruct the evolution of tissue-mediated dental biomechanics in Ceratopsia.

Occlusal morphology characterizations

Worn and unworn teeth within jaws and casts of *Triceratops* and outgroup taxa, identified using the comprehensive global phylogenies of Hailu and Dodson (50) and Makovicky (56) for Ceratopsia, and Butler and colleagues (57) for Ornithischia, were examined in the holdings of the American Museum of Natural History (AMNH; New York, NY), Mongolian Geological Museum (MAE; Ulan Bataar, Mongolia), Smithsonian Institution National Museum of Natural History (USNM; Washington, DC), Royal Tyrrell Museum of Paleontology (TMP; Drumheller, Alberta, Canada), Museum of the Rockies (MOR; Bozeman, MT), University of Alaska Museum Earth Sciences Collection (UAMES; Fairbanks, AK), and University of California Museum of Paleontology (UCMP; Berkeley, CA). The topography of the occlusal faces of the

teeth was examined and photographed. In addition, molds of worn batteries and teeth from UCMP and USNM were made with silicone putty (Silputty 40 A/B; Silpak Inc.), from which casts were made with epoxy (EpoxySet, Allied High Tech Products). The photographs and epoxy casts of these materials were used in making post hoc correlations between tissue types and modeling of wear-induced relief.

Histological and topography characterizations

Because of the uncertainties regarding the architectural makeup of dentitions in Ceratopsia, we characterized the histological composition of cheek teeth representing each morphological grade spanning their radiation. Distant outgroup Crocodylia have no occlusion (7). Thyreophora have incipient occlusion (modest and highly variable degrees of tooth-tooth contact occurring in just some teeth across the tooth rows) and provide a model for the basal ornithischian-type dentition (23). Psittacosauridae evolved low-angled shearing with variable angles between teeth along the tooth row and had teeth with enamel extending around the occlusal plane of each tooth but thicker on the leading cutting edge (44, 50). Leptoceratopsidae had equally inclined low-angled shearing teeth throughout the tooth row, but enamel became restricted to just one side of each tooth (lingual in dentary teeth and labial in maxillary teeth) edge (44, 50, 56). The clade Protoceratopsidae + Ceratopsidae retained side-restricted enamel and evolved verticalized slicing cheek teeth (44, 46). Teeth from two outgroup and four intracardal taxa were studied. These included *Leidyosuchus canadensis* (Crocodylia: AMNH 5896, $n = 2$), *Euoplocephalus tutus* (Thyreophora; AMNH FARB 32187, $n = 3$), *Psittacosaurus mongoliensis* (Psittacosauridae; AMNH/IGM MAE 97-15, $n = 12$), *Leptoceratops gracilis* (Leptoceratopsidae; AMNH FARB 32188, UAMES 34151; $n = 2$), *Protoceratops andrewsi* (Protoceratopsidae; AMNH FARB 6251, $n = 1$), and *T. horridus* (Ceratopsidae; AMNH FARB 32189, AMNH FARB 32190, $n = 2$).

Tissue compositions were determined by making petrographic slides from intact jaws and batteries and/or teeth sectioned parallel to the occlusal plane (Ceratopsia) or wear striae (*Leidyosuchus*, *Euoplocephalus*) and examined with dissecting and/or polarizing microscopy (4, 14). Microstructure was described with conventional oral histology terminology, and the distribution of tissues throughout the teeth was documented (8, 14, 58).

Histological distributions were correlated with the topography of the dinosaur teeth occlusal surfaces (see above), and the tissues responsible for various self-worn features such as basins or slicing crests were identified. The results were phylogenetically character-mapped to make evolutionary inferences regarding dental form, function, and inferred dietary properties as they relate to tissue acquisitions.

Wear rate measurements (microtribology)

Among dental material properties, relative tissue wear rate (a direct measure of material removal) is the most pertinent property to determine how dental tissues contribute to whole-tooth abrasive wear (4, 55, 59). We characterized the *Triceratops* tissue wear properties [a taxon having the entire diversity of histological types in ceratopsians (see Results)] using microtribological wear testing (Fig. 3A) on the AMNH FARB 32188 histological sections. In one experiment, a diamond-tipped probe was reciprocated across the tooth (1 mm/s, 100-mN normal force, 100 cycles per experiment). This was designed to mimic abrasive feeding strokes (4, 55). Naturally worn teeth bear coarse striae from exogenous grit and/or phytoliths [silica bodies within plants (60)], which are significantly harder than most or all dental tissues

(19). Cono-spherical diamond probes were selected as an analog of abrasive grit. For an object to act as an abrasive, it must be harder than the contacted surface and act as a rigid body (non-compliant) during loading. The actual hardness difference is inconsequential with regard to the degree of wear that is caused. Our use of a diamond, although harder than typical abrasive components of plant fodder (19), mimics these same attributes in the abrasives introduced into the dental system when ceratopsians fed.

A surface profiler (GT K1, Bruker) measured the topography of each wear scar (Fig. 3B). Volume of material removed was calculated by integrating the worn area in these profiles. An Archard wear rate $\{K [\text{mm}^3/(\text{N mm})]\}$ (61) was calculated by dividing the volume of material removed $[V (\text{mm}^3)]$ by the product of the normal force $[F_n (\text{N})]$ and sliding distance $[d (\text{mm})]$ (see Eq. 1).

$$K[\text{mm}^3/(\text{N mm})] = V[\text{mm}^3]/(F_n[\text{N}]d[\text{mm}]) \quad (1)$$

Because apatite mineral content, rather than proteins, is the major determinant of dental material properties (4, 62), they are commonly recovered in dried modern teeth (analogous to well-preserved fossils) (52, 62). We anticipated recovering these properties from the *Triceratops* specimen we sampled (AMNH FARB 32189) because it derives from the Hell Creek Formation of Montana, where well-preserved hadrosaurian teeth-preserving material properties have also been recovered (4). Indicators that biological values were recovered included correspondence of wear depths to relief on naturally worn batteries and the capacity to replicate the chewing surface topography with three-dimensional tribological models (4, 55).

Hardness measurements (nanoindentation)

Our histological-topographical analysis of the *Triceratops* teeth revealed that the bowled-out regions of the teeth are composed of highly porous vasodentine. In mammals and hadrosaurids, basin formation involving dentine occurs because of variance in hardness (a proxy for wear rate), where tissues with low hardness wear more rapidly than do harder counterparts. This led us to question whether the vasodentine's hardness, unusual porosity (giving it greater coefficients of friction), or both were responsible for its prodigious wear.

To test this question, we conducted nanohardness testing on the tissues composing the crowns and statistically contrasted the results in conjunction with the tissue wear rates. At least 25 nanoindentations (5×5 arrays) were made in each tissue with a TI 950 TriboIndenter (Hysitron Inc.). Load was increased to 5 mN at a load rate of 1 mN/s, then held at 5 mN for 5 s, and finally unloaded at a rate of 1 mN/s. A diamond Berkovich tip (radius $\sim 100 \pm 15$ nm as measured by atomic force microscopy) was used for all indentations. The indenter tip was calibrated with the Oliver and Pharr method (63) by indenting on fused quartz. Error bars in Fig. 3C represent experimental SDs.

Tooth wear modeling

The tribological model numerically simulates topographical changes in a multitissue composite *Triceratops* dental battery subjected to wear with an abrasive compliant pad analogous to ceratopsian fodder (4, 55). [Note that the exact foliage fed upon by those with occluding dentitions is not known but may have included ferns, cycads, and gymnosperm bushes and trees, and diversifying modern angiosperms (48), all of which include phytoliths (60).] The model considers the iterative coupling of wear and contact pressure (a function of surface geometry),

assuming that tissues wear in accord with Archard's wear law (61) (see Eq. 1). In each iteration, the local tissue recession [wear height, h (mm)] is the product of the local tissue wear rate, local contact pressure $[P (\text{N}/\text{mm}^2)]$, and local iterative slip distance $[\delta (\text{mm})]$ ($h = K \times P \times \delta$). This relies on the ability to calculate local contact pressure throughout the chewing surface of the tooth with a two-parameter elastic foundation contact mechanics model that was originally used in two dimensions (59) for industrial applications. This model was expanded to three-dimensional applications to encompass the greater complexity of ceratopsian, hadrosaurid, and other animal dentitions (4, 55). The model starts from a planar surface encompassing tissue distributions and empirically derived wear rates based on fossil samples (Fig. 4A). It results in an equilibrium topography, analogous to self-wear in vivo functionality (Fig. 4B). [Note that as demonstrated in our hadrosaurid wear study (4), the direction of wear does not affect the resultant topography.]

The nature of mastication with the highly sloped occlusal plane in the slicing dentition of the *Triceratops* (51) (Fig. 1C) resulted in the coronal regions (tooth crown) experiencing greater sliding distances (more time in contact) than the apical regions (root). As the jaw closed, the upper maxillary teeth initially contacted the mandibular teeth and gradually increased overlap during the feeding cycle. To simulate this increased sliding distance at the crown of the tooth, scaling slip distances (a key component of the Archard wear equation) were linearly varied from the crowns (longest slip distances) to the roots (lowest slip distances).

The tribological model was used to study the functional contributions of each tissue to the occlusal topography of the *Triceratops* dentition by considering alternative dental batteries with enamel, vasodentine, hard mantle dentine, or cementum removed from the model and with an enamel-dentine composition (primitive for Amniota) (Fig. 4, C to G). The resultant models were contrasted to infer how each dental tissue affected crest and basin formation, leading-edge sharpness, and planarity across the slicing faces of the teeth.

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